

The insect and the plant: progressive palaeoecological integration

JOHN SMART & N.F. HUGHES

*Department of Zoology, University of Cambridge, and
Department of Geology, University of Cambridge*

INTRODUCTION

The fossil record of insects (Fig. 1) starts, apart from three slightly enigmatic exceptions, in the middle of the Carboniferous, mainly in the Bashkirian but with a few examples from the Namurian (Crowson, Smart & Wootton 1967). This palaeozoic insect fauna was already diversified and while some of its important elements became extinct by the end of the Permian, or very soon thereafter, others are still extant. Odonata (*sensu lato*), Ephemeroptera (*sensu lato*), Orthoptera (*sensu lato et antiquo*) and Neuroptera were present and were joined in the Permian by representatives of Hemiptera, Coleoptera, Mecoptera and Trichoptera. A number of purely fossil orders were present of which the Megasecoptera (Carb Bashk–Perm Guad) and the Palaeodictyoptera (*sensu lato*) (Carb Bashk–Perm Guad) are the best known.

Throughout this paper we have used the contractions for geological periods and ages used in *The fossil record* published in 1967 (Harland *et al.* 1967).*

DEVONIAN INSECTS

The first of the exceptions mentioned above is the solitary specimen of *Eopterum devonicum* Rohdendorf 1961† from the upper Devonian, Komi A.S.S.R., U.S.S.R. The second, another unique fossil, is *Eopteridium striatum* Rohdendorf 1970 from 'upper Devonian beds of Belaya Tserkov (Middle Ukraine)'. In both cases the wing length would seem to be slightly under 1 cm. Both lack detail and are difficult to interpret but the Russian palaeo-entomologists, who naturally have studied them most closely, have made considerable use

* Since Harland *et al.* (1967) may not be readily available to many entomologists, the full names for the contractions mentioned are here noted: Devonian Eifelian; Carboniferous Namurian and Bashkirian; Permian Guadalupian; Triassic Norian and Rhaetian; Jurassic Bajocian; Cretaceous Barremian, Aptian, Cenomanian, Turonian and Coniacian; Tertiary Palaeocene, Lower Eocene, Middle Eocene, Upper Eocene and Lower and Middle Oligocene

† Dates are attached to authors of specific names to facilitate location of the reference in Handlirsch (1908) or the *Zoological Record*; the references are not necessarily included at the end of this chapter

of *E. devonicum* in developing their theoretical concepts of the phylogeny of the orders of insects (Sharov 1966; Rohdendorf 1969a, b). Rohdendorf (1961) erected the order Archeoptera for the reception of *Eopterum*; *Eopteridium* is placed in the same order as *Eopterum* but Rohdendorf (1970) proposes to replace the name Archeoptera with Eopterida.

The third exception is *Rhyniella praecursor* Hirst & Maulik 1926 from the famous Rhynie cherts (Dev Eifel) in Scotland. It is also a little difficult to interpret; it has been placed in the Collembola but the present trend is to regard this order as almost non-insectan (Mackerras 1970; Wallace & Mackerras 1970). It may however be noted that, to date, no one has publicly interpreted any of these Devonian fossils as anything else than terrestrial, and therefore presumably tracheate, hexapodous arthropods. Carpenter (1971) is, however, 'not convinced' from his 'examination' of the fossil that *E. devonicum* 'is an insect'.

INSECT EVOLUTION

Smart (1963) interpreted the evolution of the orders of insects as a series of radiations and published a diagram of which Fig. 1 is an up-dated version. The idea of explosive evolution occurring and producing radiations was more popular some years ago than it is today. Now it is more usual, thanks to the seminal writings of Hennig (1950, 1966, 1969), to regard almost all animal evolution as taking the form of phylogenetic dichotomies that produce 'sister' elements. This invalidates the concept of radiations in the strict sense. If, however, evolution is proceeding rapidly and we do not have before us anything approaching a series of intermediate forms, a series of close coupled dichotomies is bound to appear as a radiation in diagrams that employ the time-scales usually used when illustrating these distant phylogenetic speculations.

It may however be noted that, while we know of several orders of insects that have become extinct in the Palaeozoic or by mid-Mesozoic, no orders which have arisen since the Palaeozoic have subsequently become extinct. This could of course be due to the inevitable tendency for palaeoentomologists to place fragmentary fossils in known orders! Assessing the major extant orders, the Odonata, Ephemeroptera, Trichoptera and the Orthopteroid group have now reached a stabilized condition consistent with their specialized modes of life and long fossil history. Of these, vast numbers of the Orthopteroids are dependent on plant materials for food. Neuroptera and Mecoptera have diversified over a very long period of time and are mostly carnivorous or, perhaps, carrion feeders; they now seem to be on the decline.

It is amongst the remaining orders that the intimate relationships and inter-dependencies of the insect/plant world of today are found. The Coleoptera and Hemiptera arose in the Permian, the latter perhaps even earlier. The Hymenoptera and the Diptera are known from the early Mesozoic ('Lower' Trias and Trias Rhaet respectively), while the Lepidoptera and the Isoptera are known only from the early Tertiary though the history of both may go further back. Details of the fossil record of the major sub-divisions of the orders mentioned above will be found in Crowson, Smart & Wootton (1967).

The insect fauna of the later Carboniferous was highly diversified. There were carnivores (Odonata *sensu lato*), phytophagous and litter feeding herbivores (Orthopteroid orders), and specialized herbivores (Palaeodictyoptera, Megasecoptera—see p. 149 below). Moreover nymphs, believed to be those of Ephemeroptera, are known from the

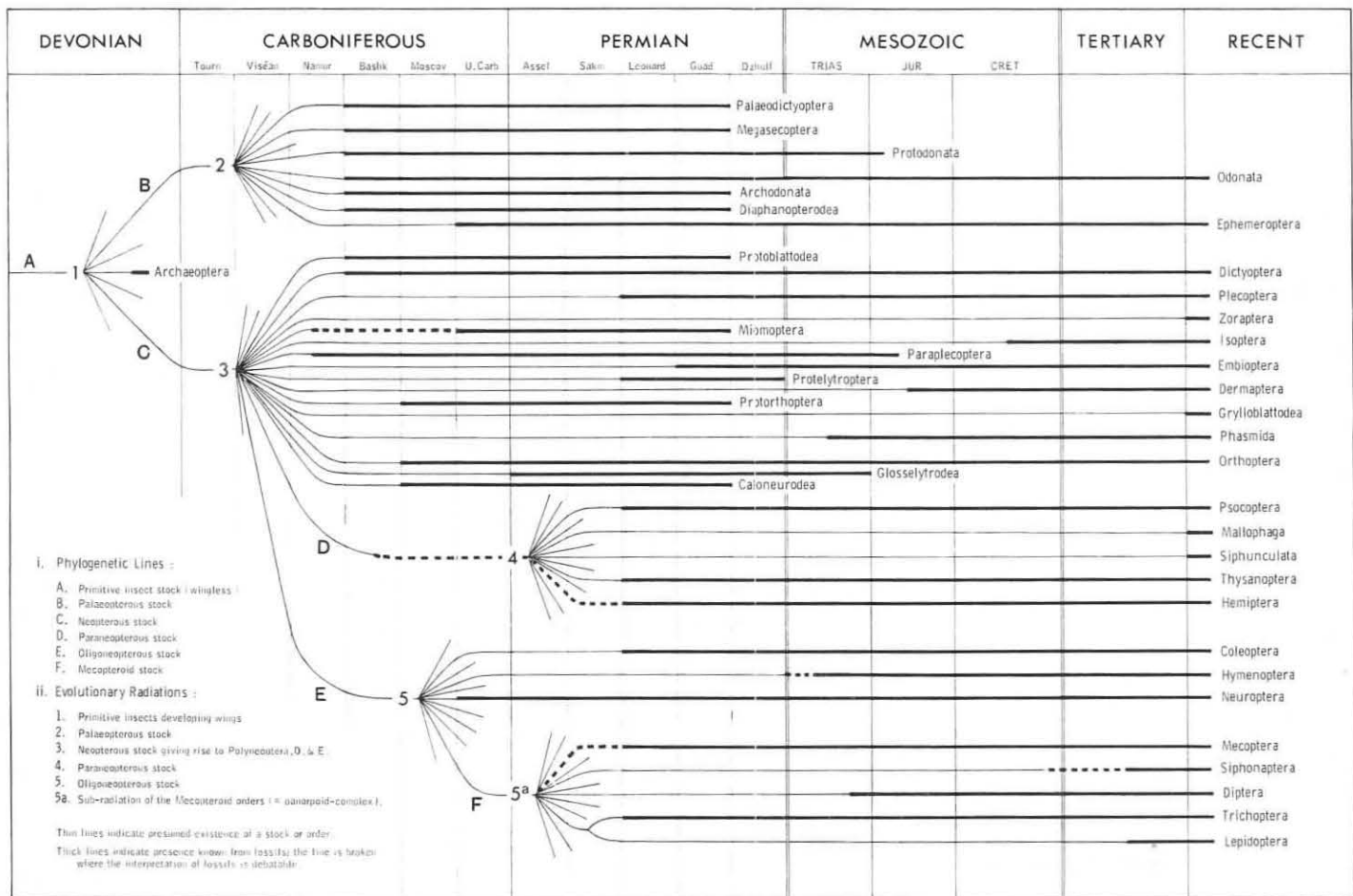


FIG. 1. The fossil record of insects and their phylogeny (modified from Smart (1963), with data from Crowson, Smart & Wootton (1967)). This figure, unlike Figs 2, 3, is not scaled for time

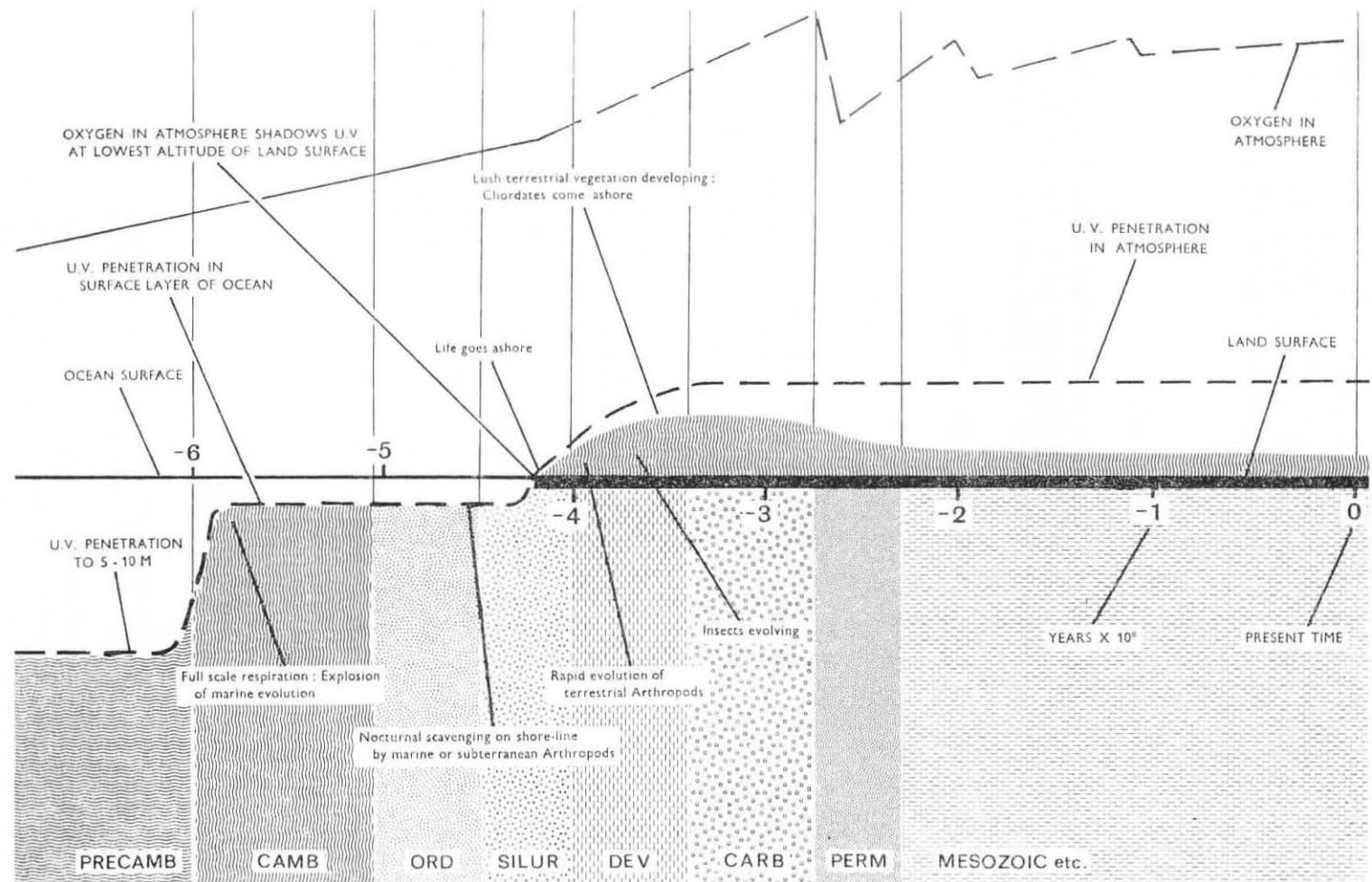


FIG. 2. Diagram illustrating events relating to the origin and evolution of insects and the relevant part of Berkner & Marshall's (1965) theory on the origin of the earth's atmosphere

Permian (Kukalova 1968), apparently completely adapted to the aquatic environment. The flora was likewise diversified and while we tend to think of the later Carboniferous as the age of the great spore-forests that gave rise to the Euramerican Coal Measures there must have been other areas, about which we know nothing, where life was more difficult for both plant and animal.

FOSSIL PLANTS

The fossil record of plants suggests that they came on land in Mid- or Late Silurian. The diversity of the insect fauna in the later Carboniferous and the occurrence of the few Devonian fossils suggest the same timing for insects. This tallies with the relevant part of

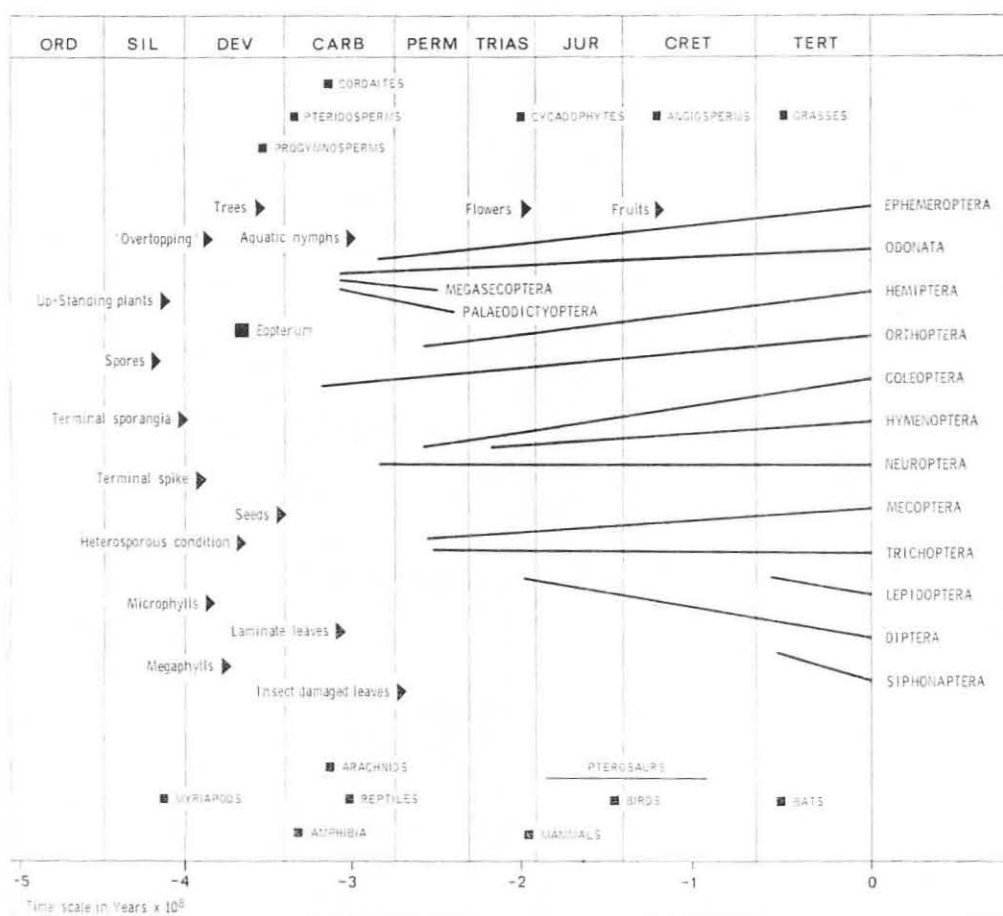


FIG. 3. Chronology of events in the development of plant and insect life (compiled from various sources including Plumstead (1963), Crowson, Smart & Wootton (1967) and Chaloner (1970))

the Berkner & Marshall (1965) theory of the evolution of the earth's atmosphere and the cutting down, by the increase in the ozone in the atmosphere, of the penetration of ultra-violet radiation to a level that would, at about this time, permit life on land at sea level exposed to sunlight (Fig. 2).

Most fossils of plant material consist of dispersed plant organs and in very few cases is the entire plant known. The chronology of the appearance of these different early plant organs has recently been most usefully summarized by Chaloner (1970). The succession of the appearance of these different plant organs is indicated in Fig. 3 along with the fossil record of some of the more important orders of insects. The relationship between plants and insects has been briefly discussed by Hughes & Smart (1967) and that between angiosperms and insects by Takhtajan (1969).

Fossil land-plant spores, appearing shortly after the middle of the Silurian, indicate the presence of terrestrial plants which were almost certainly dependent on a high water-table although there is no positive evidence that they grew in water. Fallen and decaying plant materials then, as now, could have been utilized as food either directly or indirectly by eating saprophytic fungi, etc., growing upon them. These plants could have served directly as food for mandibulate arthropods or their spores could have been utilized directly where they gathered in drifts.

The gradual development of various features of the plant body is shown in the diagram (Fig. 3). Microphylls led to megaphylls, and laminate leaves were present by the middle of the Carboniferous. Terminal sporangia are known from the Silurian-Devonian boundary, followed by their concentration into terminal spikes. The heterosporous condition made its appearance and, by the end of the Devonian, large female spores, accommodated in special parts of the plant body, were fertilized there and so became simple 'seeds'.

The earlier Devonian plants probably had a plant body that, apart from the upstanding spore-bearing stems, sprawled over the swampy ground producing a patchwork of swards of vegetation of up to a metre or so high—rather than the well-spread mixture to be seen in most reconstructions. They were probably confined to places where the water-table was high and they did not develop true roots. Here was shelter and food for insects. Whether or not the terminal spore structures were an especial attraction to them as food, and may have contributed to the evolution of the insect wing, is a matter for speculation (Smart 1967,* 1971). By the end of the Devonian, forests of trees occurred. These may have been rather more open than is usually depicted and probably much more light penetrated through the upper layers to the ground level than is the case in the modern forest.

CARBONIFEROUS PLANTS

The swamp forests that produced the equatorial Euramerican Coal Measures of the late Carboniferous, and of the Permian elsewhere, are relatively well known. There must have been other ecosystems at the time, around the margins of the swamp areas and some distance up higher ground, but these and their insect faunas are unknown to the palaeo-entomologist at the time (Carb Bashk) when the first diversified insect faunas are known from the Coal Measures. This forest must have averaged some 30 m in height; it consisted of a variety of tree-lycopods, calamites and early gymnosperms (such as pteridosperms and cordaites) with a ground flora of smaller pteridophytes. The food sources in this forest were numerous. Drifts of pollen and spores must have accumulated in places; there were stems, shoots and leaves to consume; and periodically, if not continuously, the trees and

* Recorded in Hughes & Smart (1967) as contribution to discussion

other plants must have produced crops of their diverse forms of sporangia and primitive seeds that could be utilized as food sources by active insects. On the ground there were great accumulations of rotting vegetation with its own flora of fungi and bacteria thriving on it. This forest litter, as Mamajev (1971) has pointed out, was until the appearance of the laminate leaf in mid-Carboniferous mainly an accumulation of fallen stems and branches. There must, however, also have been a great admixture of the long microphylls of *Lepidodendrales* and *Calamitales*.

Although plants with pycnoxylic wood in a complete cylinder were known from the late Devonian (*Callixylon*) and early Carboniferous (*Pitya*), stems with a single very large stele and relatively thin bark (cortex) were not an independent element of the flora until the appearance of the *Cordaitales* in the late Carboniferous (Alvin, Barnard, Harris, Hughes, Wagner & Wesley 1967). These *Cordaitales* contrasted with *Lepidodendrales* and *Calamitales* in which the stele was small in cross section or relatively so, and the cortex deep.

This relatively uniform proximity of the cambium and phloem to the stem surface in the *Cordaitales* could well have been an environmental factor in the processes of natural selection that led to the evolution of the Hemiptera with their mouthparts adapted to piercing plant tissues.

There is no direct evidence of insect/plant relationships in the Euramerican Carboniferous. The earliest evidence comes from the early Permian in the Karroo of South Africa whence Plumstead (1963) has reported leaves of *Glossopteris* in which the lamina appears to have been eaten by some insect. If we wish to get some ideas about the insect/plant relationships of the Carboniferous we are forced to make inferences from the morphology of the insects themselves.

CARBONIFEROUS INSECTS

The insect fauna of the later Carboniferous was quite diversified. Ephemeroptera were present but they seem already to have achieved the state of isolation from the other orders of insects that they have today; plainly aquatic nymphs believed to be ephemerid have been reported from the Permian (Kukalova 1968). The imagines of the earliest Odonata and of the Protodonata were the only flying predators; they seem to have been heavier in the body than are the surviving Odonata of today; their environment probably demanded less aerodynamic efficiency. The nymphs of Odonata in the Carboniferous are unknown, but the uniformity of their aquatic adaptations today suggests that the aquatic habit is of long standing. The aquatic environment would offer some relief from the pressure from predatory terrestrial arachnids.

The Orthopteroid insects were abundant and must have utilized the vegetation directly or as litter on the forest floor. Some of these were very similar to extant Orthopteroids; such are the cockroaches some of which, however, had an elongated ovipositor (Rohdendorf 1962).

There are some fossils of isolated wings or parts thereof, that suggest that ancestral Hemiptera and Mecoptera may have been present in the Carboniferous. Such, however, is the phylogenetic significance of the earliest appearance of these two orders that dating this by wings alone must be regarded as tentative no matter how exciting the results of speculations based on such datings may be.

There was, moreover, a type of insect in the Carboniferous that is not represented at all

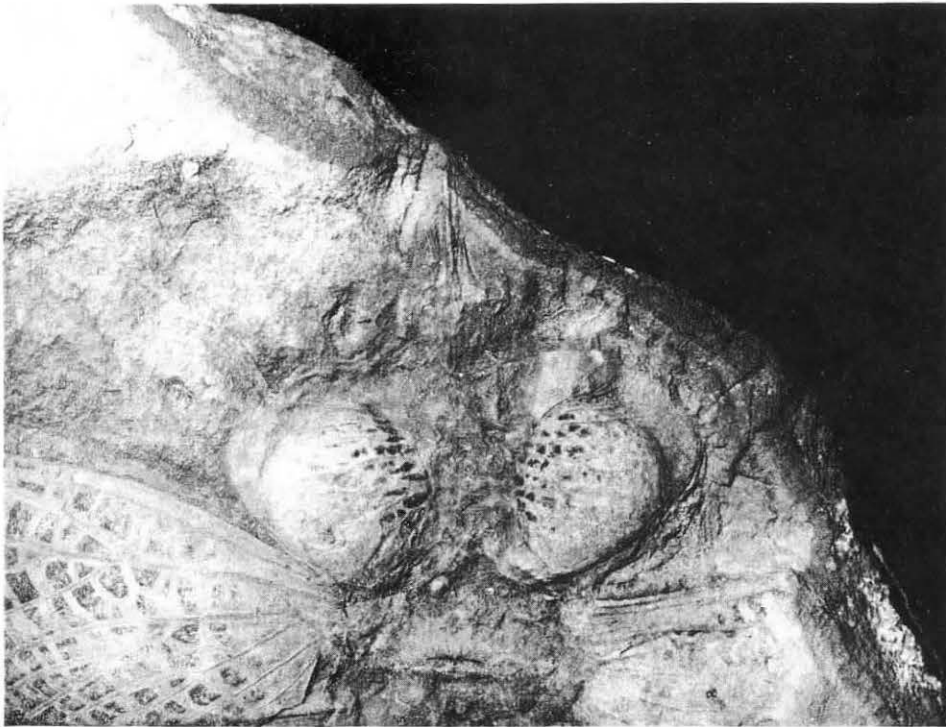


FIG. 4. *Lithomantis carbonarius* Woodward, holotype British Museum (Natural History) I.8118 from the Coal Measures of Scotland ($\times 2$). B.M.(N.H.) photo.

in the present-day insect fauna. This type was represented by the Palaeodictyoptera, Megasecoptera and two or three other less well-known groups that were probably related to them (Sharov 1971). At one time it was generally thought that these insects were rather like loosely built dragonflies. The bulk of the fossils of them are fragmentary and consist of wings or parts thereof, but slowly more information is being accumulated about them. It would seem that the mouthparts of the two orders mentioned above were probably in the form of a pointed proboscis. The proboscis can be seen in its most extreme known form in *Eugereon böckingi* Dohrn 1866 of the Lower Permian; it was also shown in the original figure of *Lithomantis carbonarius* Woodward 1876. A new photograph is reproduced here (Fig. 4).

The nymphs of Palaeodictyoptera (Sharov 1971) and of Megasecoptera (Carpenter & Richardson 1968) had proboscis mouthparts like those of the imagines and it may be implied that they lived in the same terrestrial habitat and on the same diet as the imagines and were not aquatic as has often been suggested in the past.

Laurentiaux (1952) reported on the structure of the palaeodictyopteran proboscis as he found it in a previously unstudied specimen that he identified as of the species *Stenodictya lobata* Brongniart; he illustrated his paper with two photographs of the fossil. Kukalova (1970) reported on further studies by her of this specimen; she decided it was not *S. lobata* but a new species to which she gave the name *S. laurentiauxi*. She figured the mouthparts in a line drawing and also published a line drawing of a reconstruction of *Stenodictya*. Kukalova (1970) described the mouthparts as 'haustellate' and for taking up 'liquid food only'; she does not, however, state the reasons for this conclusion. In the reconstruction she shows a prominent swelling on the head which she believes to be analagous to the post-clypeal enlargement of the head-capsule of Homoptera which accommodates the origins of the massive cibarial-pump muscles. Kukalova states that this swelling can be seen in fossils; it is not evident in the photographs published by Laurentiaux (1952).*

Eugereon was at one time regarded as the progenitor of Hemiptera solely on the basis of its proboscis. Lameere (1935) questioned this and associated *Eugereon* with the Palaeodictyoptera; this placement was confirmed by the detailed arguments later presented by Laurentiaux (1952). The best available illustrations of the proboscis of *Eugereon* are in Handlirsch (1908); it is one of the few insect fossils that the master considered worthy of photo-illustration! The Megasecoptera, often considered to be carnivores because of the raptorial nature of their prothoracic legs, have now been reported to have proboscis-like mouthparts similar to those of the Palaeodictyoptera (Carpenter & Richardson 1968).

Rohdendorf (1969a, b) has suggested, along with some other phylogenetic innovations, that the proboscis mouthparts of Palaeodictyoptera, Megasecoptera and Hemiptera indicate a common ancestry from a totally unknown and hypothetical group to be called 'Protorhynchota'. We are not convinced, however, that the proboscis of these palaeozoic insects was haustellate and for the taking up of fluids either lying free or abstracted from plant tissues in the hemipteran manner. We feel that the proboscis of these Palaeodicty-

* In November 1971, Kukalova (private communication to J.S.) drew our attention to Carpenter's (1971) paper on 'Adaptation among Palaeozoic insects'. In this paper, Carpenter agrees with Kukalova's (1970) conclusions about the mouthparts of Palaeodictyoptera and, in addition, discusses those of Megasecoptera and Diaphanopteroidea. Carpenter's illustrations of the mouthparts of Palaeodictyoptera and Diaphanopteroidea are, in fact, original line-drawings by Kukalova. The problem of the mouthparts of these insects is so important in view of Rohdendorf's (1969a, b) phylogenetic proposals (see below) that we can only hope that, at some early date, the resources of modern photography will be used to supply morphologists with the details of the data upon which Kukalova's exciting conclusions are based.

optera and Megasecoptera could have been used as a probe to work over the cones and capsules of the plants of that time for spores and pollen, and perhaps more especially for megaspores and the naked ovules of the seed ferns and early gymnosperms. Having seized such food it could then have been worked back into the mouth proper, much in the manner in which a long-beaked wading bird can be seen to work quite a small piece of food back from the tip of the beak till it can be ingested. The substrates for such feeding had been available for a long time before the actual occurrence of these insects as fossils. Phloem close to the outer surface of plant stems, suited to the hemipteran proboscis, appeared only with the Cordaitales (Carb Namur) which, however, did not reach their maximum development until the late Carboniferous (Barnard 1967) and could at that time have met the needs of evolving hemipteran stock; Rohdendorf's postulated 'Protorhynchota' have to be located right at the beginning of the early Carboniferous (Rohdendorf 1969*a, b*). Hennig (1969) has retained the orthodox view regarding Palaeoptera and Neoptera as two distinct phylogenetic lines with Paraneoptera in the latter.

THE PERMIAN PERIOD

Ecological conditions in the Permian are often presented as generally deteriorating. This is due to what seems to have happened in the area that is now roughly Europe and eastern North America. In the Cathyasian (Chinese) and the Angaran (Central Asiatic) Coal Measures of Permian age, very similar rock sequences to those of the Euramerican Coal Measures were laid down, indicating the presence of rich vegetation. There was a shift from pteridophyte dominance to gymnosperm dominance in the vegetation. Our information about insects during the Permian is considerable but much of it comes from either Kansas and Oklahoma in the U.S.A. or from 'Angara' in the U.S.S.R. The beaked Palaeodictyoptera and Megasecoptera died out and this could, perhaps, be correlated with the changes in the vegetation. These changes can also be invoked for the rapid evolution of the Hemiptera, now positively identified by fossils in which the head and proboscis are preserved (Bekker-Migdisova 1940). Fossils representing the orders Mecoptera, Trichoptera and Coleoptera are found but the variety of types of Odonata (*sensu lato*) decreases. The upland vegetation was possibly more varied than previously but again we have little or no information about it or the conditions that it provided for insects.

TRIASSIC FLOWERS

Primitive flowers come into existence when male and female organs are brought together and protected, initially, with a perianth which later spreads and appears to advertise the presence of the flower. As soon as the existence of a flower can be proven or postulated it is easy to postulate a useful rôle for visiting insects. That is to say, there arises a potential for some cross-pollination by peripatetic insects even if this be at the cost of some potential seeds being eaten as food by insects.

There is a relatively sudden appearance of the bisexual flower with the Bennettitales in the early Mesozoic (Wesley 1967) represented by *Sturiantus* (= *Sturiella*) *langeri* Kräusel in Austria (Trias Nor) followed by *Wielandiella* Nathorst, *Williamsoniella* Hamshaw Thomas (as revised by Harris 1944) and others. Some of these flowers were not originally described as bisexual but probably were so; specimens are frequently incomplete.

There is an observable size gradation in these Bennettitales flowers from *Sturianthus* (Trias Nor) about 5 mm in diameter to *Wielandiella* (Trias Rhaet) and *Williamsoniella* (Jur Bajoc) both about 20 mm, and *Williamsonia* (early Jur) and *Cycadeoidea* (early Cret) which were 10–12 cm in diameter. It even seems possible from the timing that these larger flowers may have been associated with flying vertebrates rather than insects although, in the case of *Cycadeoidea*, the flowers must have been close enough to the ground for terrestrial vertebrates to be attracted; in this case also the flower axis was not even potentially vertical.

The male organ in *Williamsoniella*, and also in *Williamsonia*, was large and thick with relatively small embedded pollen sacs. In the later *Cycadeoidea* the male structures were also large but delicate with complex branching (Delevoryas 1968; also many earlier authors). This suggests some evolution of function; it is also conceivable that these thick organs, as they developed, could have provided excess tissues that could be a source of olfactory attractants.

The ovules were very small and numerous in the earlier forms, presumably in order that losses would not cripple the reproduction of the species. For protection they were often embedded between interseminal scales; protandry may also have been involved.

The Bennettitales clearly possessed micropyles and were gymnospermous. This is reflected in the pollen which is monosulcate but had not reached the evolutionary stage of symmetrically arranged colpi correlated with the closed carpel and stigmatic receptive surfaces associated with the angiosperms. It is not known whether the Bennettitales had motile sperms such as are found in extant cycads, but this would have been a logical evolutionary step.

TRIASSIC INSECTS

When we consider the insect fauna of the Triassic period we find that it has changed markedly in some respects but remained stable in others. The litter feeders and the direct herbivores such as the Cockroaches and the Orthoptera (*sensu stricto*) are present, as are the carnivorous Odonata, the specialized Ephemeroptera and a great variety of the carnivorous Neuroptera. The phloem-feeding Hemiptera were well established in the Permian as were the Coleoptera. Diptera and Hymenoptera are found in the Trias. Fossils believed to be Trichoptera go back into the Permian.

There is, however, a very large array of fossils that are usually placed in the Mecoptera. The vast majority of these fossils are wings and in these cases it is often impossible to say positively that such wings do not belong to ancestral forms of any of the other orders that comprise the panorpoid complex (Mecoptera, Trichoptera, Lepidoptera and Diptera) except when both meso- and meta-thoracic wings are present and the Diptera are then, by definition, excluded. It is thus very likely that, at the beginning of the Mesozoic, all the orders of insects usually thought of as being associated with flowering plants were present except the Lepidoptera with their exceptional degree of morphological adaptation to feeding on the flowers of advanced angiosperms.

It should also be kept in mind that the primitive members of the orders of the panorpoid complex were probably all mandibulate. To take the most obvious example: if this had not been so, the mandibulate mosquitoes and horse flies could not have evolved if the Diptera are assumed to be a monophyletic group. The evolution of the mouthparts of Diptera has been considered in some details by Downes (1958) who also points out that extant Mecoptera, usually regarded as carnivores or carrion feeders, have been seen to

feed on flowers; Downes considers that the primitive Diptera must have been carnivores but this matter cannot be followed up here.

The ancestral Hymenoptera must, at this time, have been of a normal mandibulate type. We thus have a whole group of holometabolous insects which, in the imaginal stage, at the time when the flower of the Bennettitales arose, would be seeking a food source different from that of their larvae as the latter gradually became adapted to habitats quite unsuited to the life of the imago (the winged distributing instar of the species). Furthermore, since they were all mandibulate, they were all potential 'mess-and-soil' pollinators if they, and the then extant beetles, could be attracted to the new bisexual flowers of the Bennettitales at the right time.

Of these groups of holometabolous insects with a potential for acting as 'mess-and-soil' pollinators in the imaginal stage, we know most about the Coleoptera. Great numbers of adult beetles have been described from the Permian and this is an example where it is almost impossible to make a mistake in assigning the commonest part of the animal fossilized, the elytron, not only to the order Coleoptera but the sub-order Archestemmata to which the extant family Cupedidae belongs. The extant beetles of this family are not common; our scant information about them has been admirably summarized by Crowson (1960). The larvae live in tunnels in rotten wood; the imagines appear to be floricolous. Fossil tunnels in wood have been recorded from the Triass in the Petrified Forest National Monument in Arizona (Walker 1938) and in Germany (Linck 1949) but there is no proof that these tunnels are in fact those of larval Cupedidae.

CRETACEOUS ANGIOSPERMS

Angiosperm flowers are scarcely represented in Cretaceous rocks at all. This is no doubt due to the ephemeral nature of many of the parts of angiosperm flowers, which rendered them much more delicate than the Bennettitales flowers that had preceded them. Living representatives of the Magnoliaceae, which are often presented as typically primitive and representing the possible ancestral type of angiosperm, have relatively robust flowers but, as flowers, they are not represented in the fossil record (fossils of other parts of the plants are known from the Cret Cenom). Evidence of the presence of true angiosperms in the Cretaceous may be said to date from tricolpate pollen (Cret Apt) and recognizable angiosperm fruits (Cret Barrem).

It thus seems likely that the evolution of such advanced characteristics as secondarily unisexual flowers, secondary anemophily, zygomorphy, epigyny and the development of nectar production will have to be inferred from palynological studies and, one may hope, sooner or later more extensive knowledge of the insect fauna of the Cretaceous.

We have already alluded to the potential for error when dealing with fragmentary fossils and the tendency, be they insect or plant, to refer fragments to known taxa. There does, however, appear to have been a progressive integration between plants and insects and the chances of intelligently guiding the search for further information should be kept in mind.

CRETACEOUS INSECTS

We have already (see above, p. 151) discussed at some length the insect fauna available in the early Mesozoic. Clearly the Coleoptera were available in the Cretaceous in consider-

able variety but it should be noted that a number of groups of beetles, such as the Chrysomeloidea (Phytophaga *auctt.*) do not appear in the fossil record until the Tert M Eoc 'Mess-and-soil' pollination by Coleoptera is often presented as primitive but it is a little difficult to believe that the evolution of the bisexual flower was connected with anything so crude and haphazard. Faegri & van der Pijl (1966) had some difficulty in describing their beetle-flower syndrome, even in relation to extant angiosperms, and they admit that cantharophily is possibly secondary in flowers originally evolved for more precise pollination.

Of the other insects usually associated with flowers and their pollination, it may be noted that Hymenoptera were already present in the Cretaceous but that Aculeata, apart from ants (Cret Turon-Coniac), are not recorded till later (Tert L Eoc); bees, with their great development of labium and maxillae are later still (Tert L/M Olig). The recent discovery of these Cretaceous ants (Wilson, Carpenter & Brown 1967) does, however, suggest an earlier date for the Aculeata generally than is proven by the fossil record. Malyshev (1968) presents cogent arguments for the origin of Hymenoptera in the Palaeozoic. Diptera were likewise present in the Cretaceous, but the Cyclorrhapha are not recorded until later (Tert L/M Olig or U Eoc). Also the Lepidoptera are not recorded (except for a fossil larval head-capsule from the Cretaceous recorded by MacKay (1970)) until later (Tert L/M Olig or U Eoc); other earlier records for these insects have had to be discarded (see Crowson, Smart & Wootton 1967).

THE TERTIARY ERA

The relationship of plants and insects in the Tertiary can probably best be dealt with by backwards extrapolation from our present knowledge of the functional morphology of both groups. The following earliest known records of certain groups of plants may be of interest if related to the records given immediately above for certain groups of insects usually associated with flowering plants: Euphorbiaceae (Cret Coniac), Compositae (Tert Palaeoc), Labiatae (Tert Olig), Scrophulariaceae (Tert Olig), Papilionaceae (no Tertiary fossils) and Orchidaceae (no Tertiary fossils) (Chesters, Gnauck & Hughes 1967).

CONCLUSION

We can hope for an ever increasing precision in the fossil record of both plants and insects, though it is doubtful if we can expect anything approaching the recent progress of palynology with insect remains (which are usually fragmentary). It is a mystery why insect remains are not found in certain accumulations of dispersed plant fossil material such as those designated as 'fossil tea-leaves' by palaeobotanists. The great expansion of geological investigations that has taken place in the last few decades leads one to hope that further fossiliferous localities of insects will be discovered. We cannot, however, be over-optimistic because it seems that the conditions of sedimentation that have to occur if insect remains are to be preserved and not ground to unrecognizable fragments, are rare.

We are much indebted to Mr R.D. Norman, of the University Museum of Zoology, Cambridge, for his skilled work in the preparation of the diagrams for Figs 1, 2, 3, and to Mr S.F. Morris of the Department of Palaeontology, British Museum (Natural History), for his assistance with Fig. 4.

DISCUSSION

Dr R.J. Wootton: The emphasis of your paper has been on terrestrial insects and plants. I should be very interested to know what plants (particularly vascular plants) were likely to be available in fresh water either in the green form or as trash for the developing aquatic insects, such as the larvae of mayflies and Trichoptera, in Palaeozoic and Mesozoic times.

Mr Hughes: As far as we know there was nothing in the Palaeozoic that can be put in this category. Concerning the Mesozoic, water plants are unfortunately difficult as fossils—the megascopic parts of the plant are unlikely to be preserved as they only have little cuticle.

Professor G.C. Varley: Is there any sign of spores in the gut region of the fossil insects?

Dr Smart: I don't think there is any information whatever about the gut of Palaeozoic fossil insects. If one is postulating the consumption of spores as I was, one would of course particularly like to find a gizzard.

Dr I. Walker: What is the evidence that the leaf you mentioned was damaged by insects?

Dr Smart: The evidence is not direct. The shape of the incision on the lamina is very similar to that chewed out by perching Orthopteroids which perch on the side of the leaf and cut into it. It is clearly not a bite out of the leaf by a lizard or other reptile.

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